

EFFECT OF CHANGES IN REGIONAL FOREST ABUNDANCE ON THE DECLINE AND RECOVERY OF A FOREST BIRD COMMUNITY

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ABSTRACT.—Bird populations were monitored for 32 years in a 23-ha tract of hemlock-hardwood forest. Between 1953 and 1976 the total abundance of long-distance migrants declined significantly and four species disappeared, but after 1976 both the total abundance and the number of species increased. Multiple regression analysis shows that the abundance of long-distance migrants was negatively related to abundance of bird species characteristic of suburban habitats and positively related to the amount of forest within 2 km of the study area. The decline in long-distance migrants before 1976 occurred when suburban species were increasing and nearby forest was destroyed. The increase after 1976 is best explained by reforestation in the surrounding area because suburban birds were still increasing. A diversity of forest species, including many long-distance migrants, became established in the reforested areas. This pattern suggests that immigration from nearby forests is important in maintaining the abundance of long-distance migrants. *Received 22 Jan. 1986, accepted 10 July 1986.*

Long-term censuses of bird populations in six forest preserves in eastern North America reveal a substantial decline in both the species richness and density of migratory, forest-dwelling passerines during the past 20–30 years (Robbins 1979, Butcher et al. 1981, Leck et al. 1981, Serrao 1985). Many of the same species have declined in all of these preserves. Red-eyed Vireo, Black-throated Green Warbler, American Redstart, Ovenbird, and Hooded Warbler (scientific names are in Table 1) have decreased by 45–100% at sites where they were originally present. All sites are small urban and suburban preserves (generally <100 ha) that are isolated from other forests. Although little habitat change or direct human disturbance has occurred within the preserves, in almost all cases surrounding forest was destroyed during the period, thereby increasing the isolation of the preserves.

A greater proportion of edge habitat in small forests leads to higher rates of nest predation and brood parasitism (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985), and may result in competition with “suburban” species (i.e., species that are common in edge habitat and wooded residential areas; Butcher et al. 1981). Also, bird species may disappear because particular microhabitats are absent in a small forest (Karr 1982) or because the small populations characteristic

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of small forests are prone to local extirpation as a result of stochastic population changes (Diamond 1984). The degree of isolation from other forests may be important because nearby forests may serve as sources of immigrants to bolster declining populations, thus offsetting some of the effects of small size (Brown and Kodric-Brown 1977, Lynch and Whigham 1984). Despite this, the importance of the isolation of preserves for highly mobile animals like birds has been questioned by some researchers (McCoy 1982, Ambuel and Temple 1983). Also, Briggs and Criswell (1979) and Rappole et al. (1983) argue that the destruction of wintering habitat in the Neotropics may be the primary cause of population declines in the temperate zone.

The decline in forest bird species is particularly well documented for the Connecticut Arboretum (New London, Connecticut, USA), where periodic breeding bird censuses and vegetation surveys have been conducted since 1953. Butcher et al. (1981) describe the steep decline in forest birds between 1964 and 1976, a period when forest immediately adjacent to the study area was cut down for commercial and highway construction. Five species disappeared from the study area, and the density of three other species dropped markedly. Here we report the results of breeding bird censuses made in the same study area between 1982 and 1985, at a time when the density and species richness of forest birds had increased in the area since 1976. We suggest that this apparent recovery of the forest bird community is associated with a net increase in the amount of forest in the immediate vicinity of the study area.

STUDY AREAS

The hemlock-hardwood study area is a 23.1-ha section of the Bolleswood Natural Area in the Connecticut Arboretum at Connecticut College, New London, Connecticut (41°23'N, 72°07'W). The site is in a 61-ha tract of contiguous forest and is bisected by an intermittent stream in a small ravine. The topography is undulating, with a maximum elevation of 70 m. Hemlock (*Tsuga canadensis*) and several species of oaks (*Quercus rubra*, *Q. alba*, *Q. velutina*, and *Q. coccinea*) dominate the canopy (Niering and Goodwin 1962), which consists of large trees that survived a hurricane in 1938, and small trees that have grown up since then.

Intensive vegetation surveys have been completed along 4 permanent transects every 10 years since 1952 (Niering and Goodwin 1962, Hemond et al. 1983). The major trends have been an increase in the total basal area of trees (from 20 m² ha⁻¹ in 1952 to 37 m² ha⁻¹ in 1982) and a decrease in the density and cover of shrubs. The cover of the two dominant species in the shrub layer, *Kalmia latifolia* and *Smilax rotundifolia*, declined by more than 50% between 1952 and 1972. Gypsy moths (*Lymantria dispar*) caused extensive defoliation of the oak forest in 1982 and moderate defoliation in 1983.

Bird populations and vegetation were also monitored at a second site (the old-field study area) adjacent to the hemlock-hardwood site. This 6.5-ha plot was an open field and low thicket in 1952 (Niering and Goodwin 1962). By 1976 it was largely covered with young

forest and high-shrub thicket (Butcher et al. 1981). The transition to young forest has continued since (Niering, unpubl. data).

We completed bird surveys in a third tract (Bolles Road study area) north of the hemlock-hardwood study area on the opposite side of a paved road. This 124-ha tract is predominantly young deciduous forest with small areas of thicket and red maple swamp. Much of the area had been farmland before 1945 (Goodwin 1982).

METHODS

Bird populations in the hemlock-hardwood and old-field study areas were estimated using the spot-mapping technique (International Bird Census Committee 1969). Population estimates from 1982 to 1985 were based on 10 censuses made each year between 10 May and 8 July between 05:00 and 08:00 EDT. Total coverage per year during this period ranged from 38 to 46 h for the two study sites. From 1953 to 1976, censuses were made at approximately the same time of day and during the same weeks of the breeding season. Number of visits and coverage were also similar except for the first two censuses (1953, 1955), which involved fewer visits (7–8) and less coverage (25–32 h). Although this could result in lower estimated densities for these years (Engstrom and James 1984), results of the spot-mapping technique are robust in the range of 7–10 visits (Svensson 1978). Fractional territories were not recorded until 1973, and this could lead to somewhat higher estimates for the earlier censuses.

The spot-mapping technique is generally considered the most accurate of the standard census methods for territorial passerines (Robbins 1978). The data for this study were collected and interpreted by several observers. Best (1975) has argued that this can lead to inaccuracies, but Enemar et al. (1978) and Robbins (1978) have shown that experienced observers can obtain consistent results when they census the same plot independently.

Bird densities were estimated for the Bolles Road study areas with strip transect surveys. Singing males were mapped on a transect (1.8 km long \times 100 m wide) in 1982 and 1983 to estimate the relative abundance of breeding species. Surveys were made 2–3 times during the breeding season (23 May–17 July) between 05:30 and 09:00 EDT.

We determined the changes in total area of forest within 2 km of the center of the hemlock-hardwood study area (regional forest area) from aerial photographs (1:12,000–1:20,000 contact prints for 1951, 1965, 1975, and 1980; Natural Resources Center, Connecticut Department of Environmental Protection). For these purposes forest was defined as vegetation with a closed canopy of trees. This measure of regional forest area was used because it was an effective predictor of forest-interior bird densities for 46 forest tracts within 40 km of the study area (Askins, Philbrick, and Sugeno, unpubl. data).

Multiple regression analysis was used to determine which variables were the best predictors of population change. Previous studies indicated that forest fragmentation primarily affects forest-interior birds and long-distance migrants (Whitcomb et al. 1981, Blake and Karr 1984). We therefore analyzed the following groups of species separately: forest-interior species—territories normally restricted to interior of forest; interior-edge species—territories commonly occur both in forest interior and forest edge; edge species—primarily use forest edge or require open habitats for foraging (combines edge and field edge categories of Whitcomb et al. 1981); long-distance migrants—move to Neotropics for the winter; short-distance migrants—move to southern temperate zone or subtropics for winter; and permanent residents—remain in breeding area in winter. Classification of species into these groups is based upon Butcher et al. (1981), Whitcomb et al. (1981), and Freemark and Merriam (1986).

Combinations of 2 to 3 of the following independent variables were used in regression

analyses of population change: regional forest area, number of Brown-headed Cowbirds, number of avian nest predators (Blue Jay, American Crow, Common Grackle), and number of "suburban" species (Butcher et al. 1981). Although cowbirds and the nest predators are normally included in the suburban category, they were not included during regression analysis because they were considered separately.

RESULTS AND DISCUSSION

Between 1953 and 1976 eight species of forest-dwelling birds disappeared or declined in the hemlock-hardwood study area (Butcher et al. 1981). Seven of these species (Eastern Wood-Pewee, Red-eyed Vireo, Black-throated Green Warbler, American Redstart, Ovenbird, Hooded Warbler, Canada Warbler) are long-distance migrants (Table 1), and there was a significant decline in the total abundance of long-distance migrants (Spearman rank correlation, $r_s = -0.86$, $P < 0.05$) (Fig. 1). Short-distance migrants and permanent residents tended to increase in abundance during this period, but these trends were not significant ($P > 0.05$). The total abundance of both forest-interior and interior-edge species showed a nonsignificant tendency to decline ($P > 0.05$) (Fig. 2), while edge species increased significantly ($r_s = 0.89$, $P = 0.02$).

Between 1976 and 1985 there was an increase in the abundance of some of the long-distance migrants that had previously declined (Red-eyed Vireo, Ovenbird, Hooded Warbler). Moreover, Eastern Wood-Pewee and American Redstart, which had previously disappeared, were again present (Table 1); and Worm-eating Warbler became established for the first time (but was again absent in 1985). The total abundance of long-distance migrants did not increase significantly during this period ($P > 0.05$), but this is due to a decline in abundance after a peak in 1983 (Fig. 1). Forest-interior and interior-edge species also tended to increase in abundance after 1976 (Fig. 2), but these trends are not significant ($P > 0.05$). However, the density of Red-eyed Vireo (originally the most abundant long-distance migrant) did increase significantly ($r_s = 1.0$, $P = 0.05$) (Table 1).

The decline in abundance of long-distance migrants occurred at the same time that the amount of forest near the study area was reduced, whereas the subsequent, apparent increase in abundance occurred when the amount of nearby forest increased. Regional forest area decreased from 418 ha to 363 ha between 1951 and 1975 due primarily to commercial development south of the study area, and increased to 464 ha by 1985 due to growth of forest on abandoned farmland in and around the Bolles Lane and old-field study areas.

In multiple regression analyses the abundance of all long-distance migrants and of long-distance migrants in the forest-interior and interior-

edge categories (hereafter referred to as forest long-distance migrants or FLM) were both used as dependent variables. We report on the results for FLM species because this group is more pertinent to a discussion of changes in forest bird populations. The results for the two variables, however, were similar.

Regression analysis showed that between 1953 and 1985 the total abundance of FLM species was positively correlated with regional forest area ($F = 10.2$, $P < 0.05$) and negatively correlated with abundance of suburban species ($F = 12.8$, $P < 0.02$). The other independent variables (number of cowbirds and number of avian nest predators) did not have significant partial regression coefficients.

The positive relationship between the abundance of long-distance migrants and the amount of forest within 2 km of the study area is consistent with the hypothesis that the composition of forest bird communities is directly affected by the degree of isolation from similar communities that might serve as a source of immigrants. Between 1953 and 1985 the abundance of forest long-distance migrants increased significantly in abandoned farmland of the old-field study area ($r_s = 0.81$, $P < 0.01$); by 1982, nine species were present (Fig. 3). Aerial photos show that the sequence of vegetation change in the Bolles Road study area was similar to the sequence in the old-field study area. By 1982 this northern tract was a mosaic of young and older forest, and a large number of species of forest birds (including the species that had increased in the hemlock-hardwood study area) were detected on transect surveys of the tract in 1982 and 1983 (Table 2). Thus, over the course of our study, the hemlock-hardwood study area was becoming less isolated from other forest bird communities.

The abundance of FLM species declined during a period of deforestation and increased during a period when forest grew up and forest bird communities became established nearby. Both the reduction and increase in regional forest area were small (13% and 28%, respectively), but in both cases tracts immediately adjacent to the study area were affected. The proximity of other forest bird communities could determine the rate of dispersal into the study area, which in turn could determine whether some species maintain viable populations or become reestablished.

The negative relationship between suburban species and FLM migrants is consistent with the hypothesis that the influx of suburban species into small forests has a negative impact on migratory forest birds (Butcher et al. 1981, Whitcomb et al. 1981). Between 1953 and 1985 the density of suburban species increased ($r_s = 0.90$, $P < 0.001$) while that of FLM migrants declined ($r_s = -0.74$, $P < 0.05$). Abundance of suburban species was not correlated with regional forest area ($r_s = 0.52$, $P > 0.05$) and was a significant predictor of abundance of FLM migrants even when regional

TABLE 1
CONTINUED

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Interior-edge species											
Long-distance migrants											
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	0	0	0	0	0	0	0	1	0	0.5	0
Yellow-billed Cuckoo (<i>C. americanus</i>) ^a	0	0	0	0	0	1	0	1	0.5	0	0
Eastern Wood-Pewee (<i>Contopus virens</i>) ^a	3	1	1	3	3	0	0	3.5	1	3	2
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	0	0	1	3	2	4	4	4.5	4	5	3
Wood Thrush (<i>Hylocichla mustelina</i>) ^a	7	10	12	9	1	7	5	5.5	6.5	2	2.5
Red-eyed Vireo (<i>Vireo olivaceus</i>)	20	22	16	21	17	2	4	10	13	14	15
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	0	0	0	0	0	0.5	0	0.5	0	0	0
Short-distance migrants											
Northern Flicker (<i>Colaptes auratus</i>) ^a	2	1	1	1	2	2.5	0	1.5	1	0.5	1
Eastern Phoebe (<i>Sayornis phoebe</i>)	1	1	1	0	0	0	1	2	0	1	1
Gray Catbird (<i>Dumetella carolinensis</i>) ^a	9	8	6	9	10	9.5	10	7.5	9.5	9.5	9.5
White-eyed Vireo (<i>V. griseus</i>)	0	1	2	0	0	0	1	2	0	0.5	2.5
Common Yellowthroat (<i>Geothlypis trichas</i>)	5	2	2	2	3	1	2	3.5	3.5	6	2
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	7	9	15	15	13	10	7	5.5	10	4.5	7.5
Permanent residents											
Ruffed Grouse (<i>Bonasa umbellus</i>)	1	1	1	0	2	1	0	0	0	0	0
Downy Woodpecker (<i>Picoides pubescens</i>) ^a	0	0	0	0	0	2	0	2.5	2.5	2	2
Blue Jay (<i>Cyanocitta cristata</i>) ^{a,b}	1	2	4	4	3	7	2	5.5	4	4	1
Black-capped Chickadee (<i>Parus atricapillus</i>) ^a	3	2	4	5	5	7	2	10	11.5	11.5	11.5
Tufted Titmouse (<i>P. bicolor</i>) ^a	0	0	0	0	0	0	5	7.5	8	9.5	9.5
Carolina Wren (<i>Thryothorus ludovicianus</i>) ^a	0	1	1	0	0	0	0	0	0	0	0
Northern Cardinal (<i>Cardinalis cardinalis</i>) ^a	0	0	0	0	1	1	1.5	7	4	3	3

TABLE 1
CONTINUED

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Edge species											
Long-distance migrants											
Whip-poor-will (<i>Caprimulgus vociferus</i>)	1	0	2	1	0	0	0	0	0	0	0
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	0	0	0	0	0	0	0	0	0	0.5	0
Blue-winged Warbler (<i>Vermivora pinus</i>)	1	1	0	0	3	0	1	2	2.5	3	1.5
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	1	1	0	0	3	1.5	0	2.5	1.5	1.5	1.5
Prairie Warbler (<i>D. discolor</i>)	0	0	1	0	0	0	0	0	0	0	0
Indigo Bunting (<i>Passerina cyanea</i>)	0	0	0	0	0	0	1	0	0	0	0
Northern Oriole (<i>Icterus galbula</i>) ^a	0	0	0	0	0	2.5	4	1.5	1	0.5	0
Short-distance migrants											
Mourning Dove (<i>Zenaida macroura</i>) ^{a,b}	0	0	0	0	2	0	0	1.5	0	0	0
House Wren (<i>Troglodytes aedon</i>) ^a	1	1	2	4	8	5	8.5	6.5	7	6	10
American Robin (<i>Turdus migratorius</i>) ^a	0	0	0	2	1	1	1	0	0	0	0
Brown Thrasher (<i>Toxostoma rufum</i>) ^a	0	0	2	0	1	3	1	0	0	0	0
Chipping Sparrow (<i>Spizella passerina</i>)	0	0	0	0	0	0	0	0	0	1	0
Song Sparrow (<i>Melospiza melodia</i>)	0	0	0	0	0	0	0	0	1	0	0
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	0	0	0	0	1	4	1	2	2	0	0
Common Grackle (<i>Quiscalus quiscula</i>) ^{a,b}	0	0	0	1	0	0	0	0	0	0	0
Brown-headed Cowbird (<i>Molothrus ater</i>) ^{a,c}	0	0	0	0	1	0	0	9.5	2.5	1.5	2
	(0)	(6)	(1)	(1)	(2)	(1)	(2)	(69)	(33)	(22)	(13)

TABLE 1
CONTINUED

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Permanent residents											
Northern Bobwhite (<i>Colinus virginianus</i>)	0	1	0	0	0	0	0	0	0	0	0
American Crow (<i>Corvus brachyrhynchos</i>) ^a	0	0	2	2	1	0	0	0	0	2.5	1

^a Suburban species (i.e., characteristic of wooded residential areas; Butcher et al. 1981).

^b Because males do not defend a large territory, the estimated number of breeding pairs is indicated.

^c Repeated observations of cowbirds in one area may indicate a female territory, but this is difficult to confirm as females are more secretive and silent than males (Duffy 1982). Therefore, to provide another measure of abundance, the total number of separate observations of cowbirds is shown for each year (in parentheses).

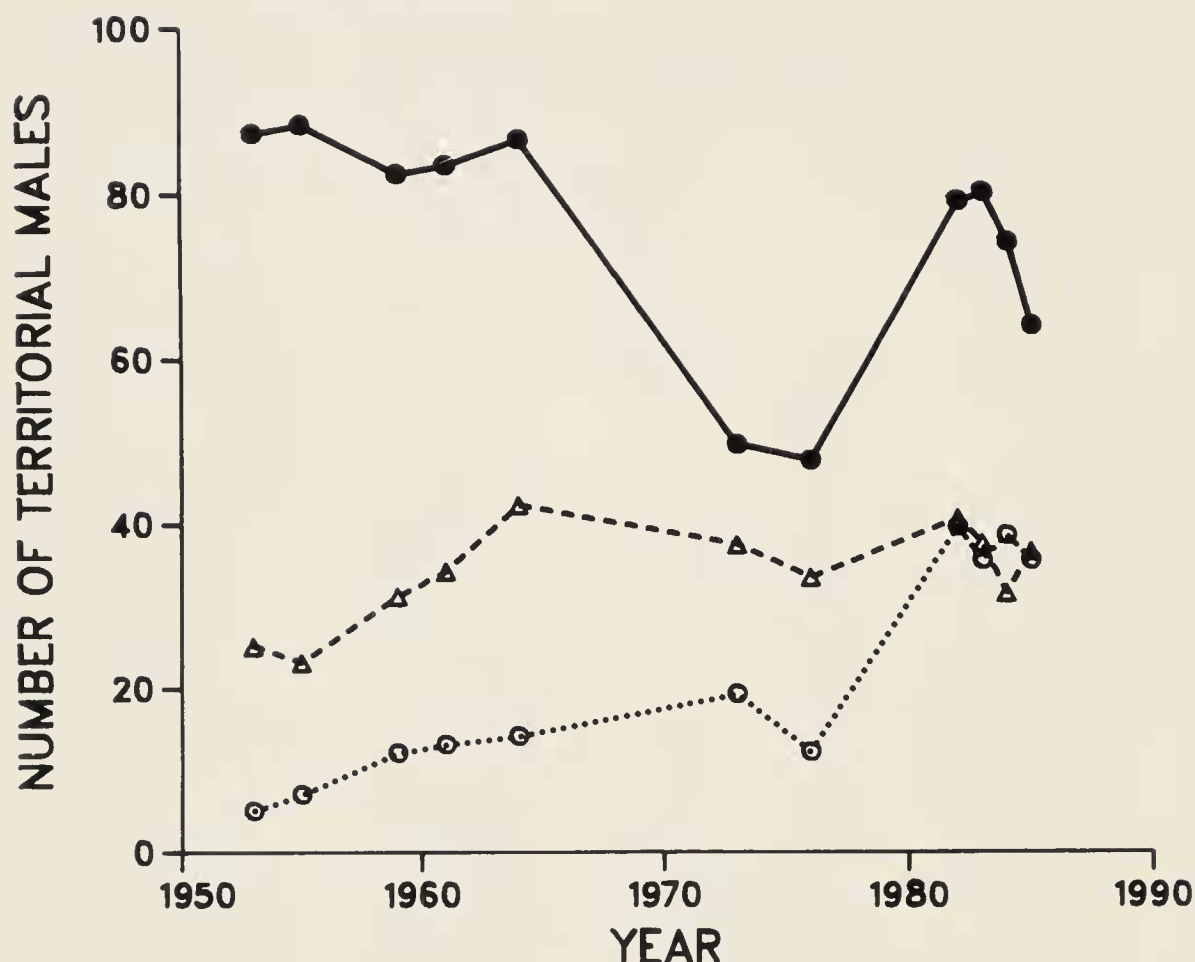


FIG. 1. Change in total population for long-distance migrants (solid line), short-distance migrants (dashed line), and permanent residents (dotted line).

forest area was controlled for in multiple regression analysis. Suburban species increased from 46 to 57 territorial males between 1976 and 1985 as regional forest area increased.

Most of the increase in abundance of suburban birds was due to three species: Black-capped Chickadee, Tufted Titmouse, and House Wren (Table 1). All are foliage-gleaning insectivores, and thus are possible competitors with the FLM species that declined, most of which are also foliage-gleaners (six species of vireos and wood warblers). Populations of Black-capped Chickadee and Tufted Titmouse appear to have increased regionally, perhaps as a result of suburban bird feeders (Kricher 1981). Also, Tufted Titmouse expanded its range northward into Connecticut during the period (Kricher 1981, Loery and Nichols 1985). A regional increase in these foliage-gleaners could lead to a decline in FLM species with similar feeding behavior, but the FLM decline is not necessarily related causally to the increase in suburban birds. Suburban species may have increased due to competitive release after the FLM decline (Whit-

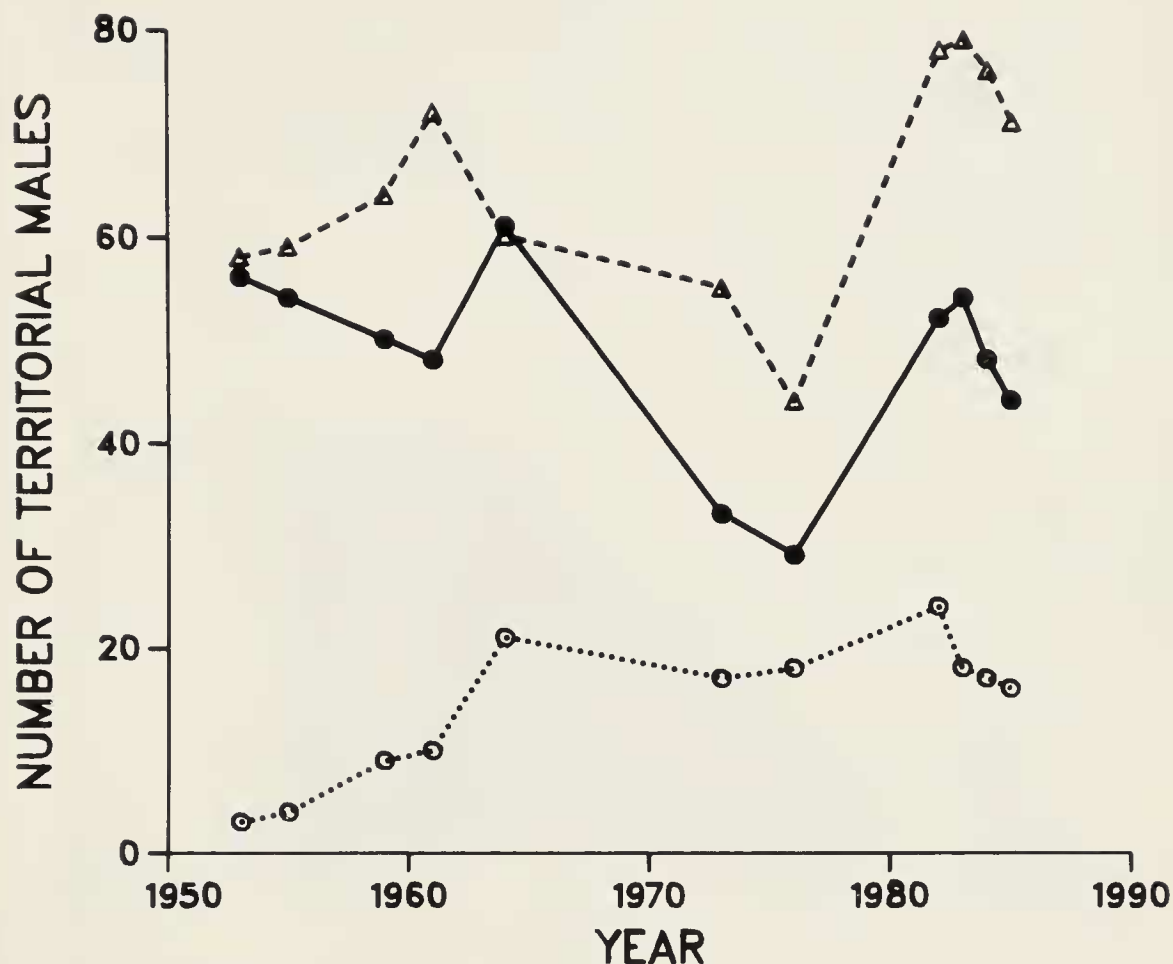


FIG. 2. Change in total population for forest-interior species (solid line), interior-edge species (dashed line), and edge species (dotted line).

comb et al. 1981), or both groups may have been responding to habitat change in and around the study area.

The shrub layer became less dense between 1953 and 1973 (Hemond et al. 1983), and this is a potential factor in the decline of American Redstart, Canada Warbler, and Hooded Warbler, species that nest and feed in this layer and the understory (Bent 1953, Anderson and Shugart 1974, Seidel and Whitmore 1982). The Hooded Warbler population increased between 1976 and 1985 as the shrub layer became even less dense (Niering, unpubl. data), so thinning of the shrub layer does not entirely account for its previous decline. Habitat change may account for the decline of the other two species, which showed little or no increase during this period. However, the abundance of FLM migrants is still related to both regional area and abundance of suburban species when these two species are not included in the analysis ($F > 10$, $P < 0.05$ for both variables).

Red-eyed Vireo, Ovenbird, and Black-throated Green Warbler declined

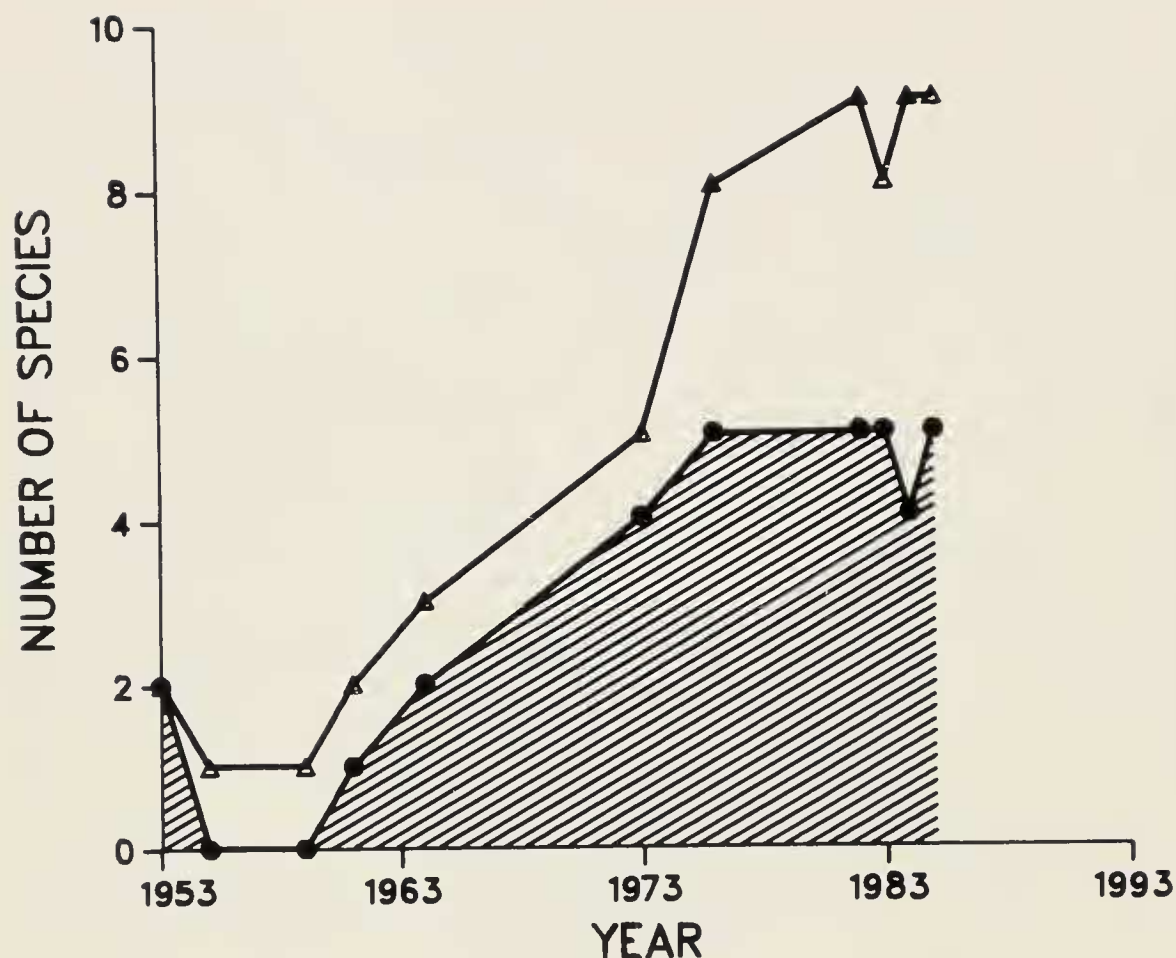


FIG. 3. Change in the number of species of interior-edge birds (unshaded) and forest-interior birds (shaded) in the old-field study area during a period of transition from open field and low thicket to young forest.

despite an apparent increase in favorable habitat (closed canopy forest, Clark et al. 1983). In fact, between 1953 and 1985 the total abundance of FLM species was negatively correlated with total basal area of trees ($r = -0.66$, $P < 0.05$), indicating that these species declined despite the maturation of the forest (i.e., larger trees and an associated decrease in the density of trees and shrubs; Hemond et al. 1983).

Brittingham and Temple (1983) argue that brood parasitism by Brown-headed Cowbirds may be a major factor in the decline of forest bird populations in small forest patches in the eastern United States. Brown-headed Cowbird abundance was not significantly related to FLM abundance in the Connecticut Arboretum. Cowbird abundance was low during the period of FLM decline, but was considerably higher during the 1980s (perhaps due to high densities of gypsy moth caterpillars, Smith and Lautenschlager 1981), when FLM birds had increased. Only the small

TABLE 2
COMPARISON OF POPULATION DENSITIES OF LONG-DISTANCE MIGRANTS IN THE
HEMLOCK-HARDWOOD AND BOLLES ROAD STUDY AREAS

Species ^a	Estimated density (males or pairs/10 ha)			
	Hemlock-hardwood ^b		Bolles Road	
	1982	1983	1982	1983
Eastern Wood-Pewee	1.5	0.4	1.7	1.1
Red-eyed Vireo	4.3	5.7	6.1	6.7
American Redstart	0	0.4	0	0
Worm-eating Warbler	0.4	0.4	0.6	1.1
Ovenbird	5.9	6.5	1.7	5.0
Hooded Warbler	0	0.7	2.2	2.2

^a Only FLM species that increased in abundance in the hemlock-hardwood study area between 1976 and 1985 are included.

^b The hemlock-hardwood study area includes 23 ha and the Bolles Road study area includes 124 ha.

decline in long-distance migrant abundance in 1984–1985 (Fig. 1) is likely to be due to cowbird parasitism.

High nest predation rates in small, suburban forests have been demonstrated experimentally (Wilcove 1985). Although the abundance of avian nest predators is not related to FLM abundance, we have no data on mammalian predators.

Our results suggest that the abundance of forest-dwelling, long-distance migrants is related to the abundance of suburban species and to regional forest area. Long-distance migrants declined during a period when suburban species were increasing and when forest close to the study area was destroyed. After 1976, however, the populations of several species of long-distance migrants increased. This partial recovery occurred during a period when the abundance of suburban species was still increasing, but when areas of thicket near the study area changed to young forest. Of the six forest tracts in the northeastern U.S. in which a general decline in forest birds has been documented during the past 20–30 years, the Connecticut Arboretum is the only site where populations of several species have recently recovered. It is also the only site for which reforestation in adjacent areas has been reported (Robbins 1979, Leck et al. 1981, Serrao 1985). This suggests that populations of many species are not self-sufficient in a small preserve, but instead are part of a larger, regional population (Ambuel and Temple 1983). Thus, extensive deforestation in the vicinity of a preserve may cause populations of these species to decline and might result in their extirpation.

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